

## BRIEF COMMUNICATIONS

# Mice (*Mus musculus*) Learn a Win–Shift but Not a Win–Stay Contingency Under Water Escape Motivation

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Twenty mice (*Mus musculus*), the second filial generation offspring from a C57BL/6 and DBA/2J cross, received spatial win–shift and win–stay water escape training within a mixed design in which all mice received both types of training. Acquisition under win–shift was superior to win–stay with respect to errorless trials and latencies regardless of the order in which the procedures were experienced. Win–stay responding did not exceed chance levels during any training phase. These data contradict the claim that win–stay training is the more easily acquired of the 2 acquisition strategies under aversive motivation.

Procedures that involve win–shift (nonmatching to sample) and win–stay (matching to sample) strategies have become common techniques with which to assess complex problem solving. These procedures have proven useful in the study of rudimentary concept formation (same or different) and in the tapping of working memory to the extent that they require a subject to use responses to prior stimuli when subsequently faced with a choice between prior stimuli and new stimuli. As both procedures presumably draw on common processes, these procedures might be expected to be acquired at the same rate.

A number of studies have systematically examined this expectation. Although these studies are not entirely uniform in their findings, the majority of them have found that win–shift strategies are more readily acquired than are win–stay strategies using positive reinforcement, suggesting that the two procedures should not be considered identical (Gaffan & Davies, 1981; Means, 1988; Olton & Schlosberg, 1978). In support of this conclusion, physiological work suggests that win–shift and win–stay learning are affected differentially by lesions to the same areas (e.g., McDonald & White, 1993; Packard & White, 1990).

The advantage of win–shift over win–stay has been attributed to the tendency, particularly among rodents, to forage by avoiding previously visited food patches (see Olton & Schlosberg, 1978, for a discussion). An alternative interpretation that does not rely on foraging strategies or on the presence of food focuses on the tendency of many species to engage in spontaneous alternation in a situation in which a subject confronts two choices, one of which has previously been explored (Gaffan & Davies, 1981). This second interpretation makes use of optimal arousal theory by

incorporating the idea that the choice of new alternatives as opposed to familiar alternatives increases arousal. A corollary of this approach predicts that under conditions of high arousal, such as those found in aversive conditioning, animals might avoid increased arousal and instead choose familiar alternatives. Means (1988) tested this hypothesis in a water escape procedure with rats and found that win–stay learning was more rapidly acquired than was win–shift learning. Mitchell, Koleszar, and Scopatz (1984), while noting strain differences between CBA and NZB mice, observed an overall treatment effect of stress (shock) versus no stress within a spontaneous alternation procedure. Their no-stress condition produced relatively high levels of spontaneous alternation, whereas their stress condition led to perseveration, that is, the consistent choice of a particular location (right or left) irrespective of goal location.

Preferences for win–shift or win–stay strategies have often been interpreted within a comparative framework. Means (1988) concluded that “response perseveration and win–stay are more natural responses than win–shift for rats in a water escape situation” (p. 303). Olton and Schlosberg (1978), in summarizing data regarding win–shift preferences in rats, referred to the importance of “considering animals’ species-specific dispositions in designing tests of cognitive abilities” (p. 617). Similarly, Randall and Zentall (1997) referred to rats’ “natural predisposition to avoid recently visited locations” (p. 227) and summarized their own evidence taken from studying pigeons in a modified win–stay/win–shift procedure as indicating that “unlike rats, pigeons may be somewhat predisposed to repeat a response to a location to which responses have been previously rewarded” (p. 227).

Despite these sorts of generalizations, a number of investigators have observed that the advantage of win–shift over win–stay in appetitive situations is not uniformly found across different species. The results of some comparative studies using goldfish (Goldman & Shapiro, 1979), common marmosets (MacDonald, Pang, & Gibeault, 1994), and honey bees (see Figures 1a and 3a in Giurfa, Zhang, Jenett, Menzel, & Srinivasan, 2001) and other studies using pigeons (e.g., Hughes, 1989; Wright & Delius, 1994; but see Olson & Maki, 1983) have indicated either no difference

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between win-shift and win-stay strategies or a preference for win-stay using positive reinforcement.

It is also demonstrable that as with other learning phenomena, procedural variations strongly affect preference for win-shift/win-stay. Herrmann, Bahr, Bremner, and Ellen (1982), for example, using a version of Maier's classic three-table problem with rats, found better win-stay learning under conditions of partial feeding as the reinforcer (i.e., less than the daily intake needed to maintain weight), but better win-shift learning with complete feeding. Comer and Means (1989) noted a similar effect of procedural changes in a follow-up of Means's (1988) original study. Means and Fernandez's (1992) results indicated that win-shift and win-stay strategies could both be acquired by rats using water escape motivation, although win-stay learning was still accomplished more rapidly than win-shift learning. Despite the success of their procedural manipulations to lessen the differences between win-shift and win-stay training, Comer and Means (1989) concluded that "win-stay is the more natural, automatic response in water-escape tasks" (p. 247).

These studies on the effects of procedural manipulations on win-shift and win-stay learning, along with the comparative studies cited earlier, suggest caution with respect to forming generalizations regarding the superiority of one strategy over the other. The study reported herein assessed one such generalization: the conclusion that rodents prefer win-stay learning under conditions of aversive motivation. We studied win-stay and win-shift learning using mice and water escape motivation. Data were collected on the influence of the preexperimental tendencies of mice to alternate on successive trials via a spontaneous alternation task. We also assessed the preference of mice for particular locations by measuring perseveration during win-shift and win-stay training.

## Method

### Subjects

Twenty experimentally naive mice (*Mus musculus*) were used. Mice were the second filial generation (F<sub>2</sub>) derived from a cross between C57BL/6 and DBA/2J inbred strains. We used this particular F<sub>2</sub> cross because one of our long-term interests is the study of individual differences. The parental inbred strains have repeatedly been shown to differ markedly in learning and memory abilities (e.g., Thinus-Blanc, Save, Rossi-Arnaud, Tozzi, & Ammassari-Teule, 1996). The F<sub>2</sub>s derived from this cross were likely to possess considerable individual differences with respect to learning and memory tasks. The prior work of Locurto and Scanlon (1998, Table 1, p. 347) with these F<sub>2</sub>s indicated that their variability is equivalent to if not greater than the variability of CD-1s, an explicitly outbred strain. Additionally, our laboratory has substantial prior experience using these mice in win-shift and other problem-solving tasks (Markowski, Ungeheuer, Bitran, and Locurto, 2001).

Mice were experimentally naive and were approximately 2.5 months old at the start of the study. There were an equal number of males and females tested. They were maintained on a 12-hr reversed-diurnal cycle that was keyed to 6 a.m. and 6 p.m. local time. Testing occurred in a room illuminated by two 35-W fluorescent tube lights located 7.4 m above the testing arenas. Testing occurred at least 2 hr into the dark cycle. Food and water were constantly available in the home cages.

### Apparatus

Spontaneous alternation was carried out as a water escape task in a T-maze constructed of black Plexiglas. The maze was 30.5 × 38.0 × 15.2

cm. Win-stay and win-shift learning were carried out in a Y-maze with identical arm measurements to the T-maze. Platforms measuring 15.2 × 10.2 × 14.6 cm were placed just below water level in the designated correct arm or arms on a given trial. Water temperature was maintained at 26 °C ± 1 °C.

### Procedure

*Spontaneous alternation.* Spontaneous alternation was the first task for all mice. Two sessions of habituation to the T-maze preceded training. During habituation, mice were allowed to explore the apparatus, and escape platforms were provided in both goal arms. If a mouse did not find a platform within 60 s, it was placed on the platform for 10 s. Each mouse experienced 3–4 trials during each habituation session.

Spontaneous alternation training took place over five consecutive sessions with five trials per session. Neither arm of the T-maze contained a platform during spontaneous alternation training. Each trial consisted of two runs: For the first run, the mouse was allowed to choose either arm of the T-maze. Once the mouse had passed more than halfway down an arm, that arm was blocked for 10 s. The mouse was then returned to the start arm and allowed another free choice, following a 10-s intertrial interval (ITI). An alternation was recorded when a mouse chose the arm that was not visited during the first run.

*Win-stay/win-shift.* Two days of habituation to the Y-maze preceded training. Habituation training was conducted in the same manner as was habituation prior to spontaneous alternation. All mice were given 15 sessions of win-stay and 10 sessions of win-shift. These differing training periods reflect the relative rapidity with which each procedure was learned: As is detailed later, at the end of the first 10 sessions under win-stay training, responding was not above chance, and the decision was made to continue training for 5 additional sessions.

Each session consisted of 10 trials, and each trial consisted of three runs. A trial began with two sample runs in which the mouse was forced to choose either the left or the right arm twice in succession, with the other choice blocked. Following these two forced-choice runs, a free-choice run was given in which the mouse could choose either arm. The location of correct arms was determined using a table of random numbers, with the restriction that one location (left or right) could not occur more than three trials in a row during a session. Mice had 60 s to locate the correct arm that contained an escape platform. If a mouse did not locate the arm in the allotted time, then that mouse was placed on the platform at the end of 60 s so that each run terminated with an escape. Mice were left on the escape platform for 10 s at the end of each forced-choice run and for 20 s at the end of each free-choice run before the next trial was initiated. Each mouse was run for 10 consecutive trials before the next mouse was run. In win-stay training, the correct choice was the same arm that was correct during forced-choice runs. In win-shift training on free-choice runs, the arm opposite the forced-choice arm was correct.

Half of the mice experienced the sequence win-stay for 15 sessions followed by win-shift for 10 sessions (stay-shift group). The remaining half of the mice experienced the reverse order of these procedures (shift-stay group). Errors were defined as entries past the midpoint of the incorrect arm or reentries into the start arm that crossed the midpoint of that arm.

## Results

There were no significant sex differences. As a result, sexes were combined within groups for all data analyses. Figure 1 presents errorless trials (i.e., correct responses during free-choice runs) for each group during each session. It is clear that acquisition was much more rapid and that terminal levels of errorless trials were much higher during win-shift than during win-stay training. This finding was true for each phase (pre and post) of the reversal

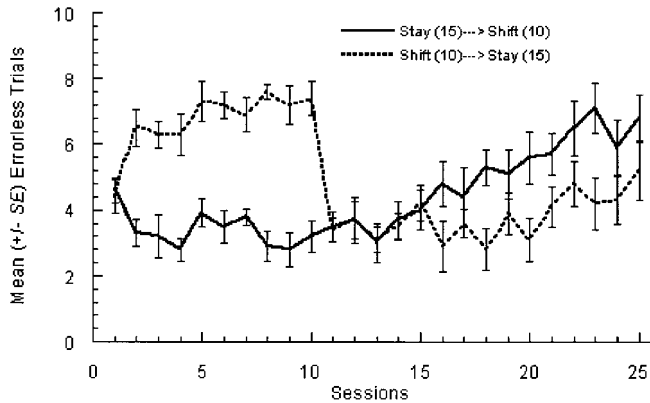


Figure 1. Mean ( $\pm$  SE) errorless trials for each session. Numbers in parentheses in legend indicate the number of sessions of training for each procedure.

procedure. Despite these average differences, there was a significant correlation between mean errorless trials across procedures,  $r(18) = .43$ ,  $p < .05$ , one-tailed.

A mixed-design analysis was applied to the common sessions (Sessions 1–10) in each phase. For the prereversal portion of training, results indicated a significant difference between groups,  $F(1, 18) = 73.65$ ,  $p < .01$ , and a significant Sessions  $\times$  Groups interaction,  $F(9, 162) = 5.07$ ,  $p < .01$ . There was no main effect for sessions ( $p > .05$ ). The significant interaction term for this prereversal phase reflected the rapid acquisition of responding under win–shift as compared with the chance-level responding under win–stay.

Analysis of the additional 5 sessions given to win–stay mice in this phase indicated that average errorless trials were significantly higher compared with the 5 preceding sessions,  $t(9) = -1.84$ ,  $p < .05$ , one-tailed. However, overall, there was no significant sessions effect for this group either for the 10 common sessions or for when the additional 5 sessions were included ( $p > .10$ , for both analyses). During the 15 sessions of win–stay training, mean errorless trials averaged 3.46, a value that was significantly less than the chance value of 5.0,  $t(14) = -11.80$ ,  $p < .01$ .

For the postreversal phase of training, again the first 10 common sessions (Sessions 16–25 for the stay–shift group, Sessions 11–20 for the shift–stay group) for each group were compared. Analysis indicated a significant difference between groups,  $F(1, 18) = 10.49$ ,  $p < .01$ , and a significant Groups  $\times$  Sessions interaction,  $F(9, 162) = 3.13$ ,  $p < .05$ . Again, there was no overall significant effect of sessions ( $p > .10$ ). Analysis of the 5 additional sessions given to the shift–stay group in this phase indicated that average errorless trials were higher during these added sessions as compared with the 5 preceding sessions,  $t(9) = -2.28$ ,  $p < .05$ . Although there was no significant sessions effect for this group during the 10 common sessions ( $p > .10$ ), there was a significant sessions effect when the additional 5 sessions were included,  $F(14, 126) = 2.04$ ,  $p < .05$ . However, errorless trials averaged 3.79 across the 15 win–stay sessions for the shift–stay group, a value that was significantly below chance,  $t(14) = -6.78$ ,  $p < .01$ . This value did not differ from the win–stay performance of the stay–shift group ( $p > .10$ ).

To assess whether there was an effect of order of treatment, we compared responding between groups within procedures (e.g., win–stay vs. win–stay, win–shift vs. win–shift). No differences were observed in this analysis for groups ( $p > .05$ ) or for the Sessions  $\times$  Groups interactions ( $p > .05$ ) for either procedure. This pattern of findings indicates that performance was comparable within each procedure irrespective of when that procedure occurred.

Figure 2 presents latencies for each group during each session. Latencies were clearly lower during win–shift compared with win–stay within each phase of training. As was true for errorless trials, despite these average differences, there was a significant correlation in latencies across procedures,  $r(18) = .84$ ,  $p < .01$ , one-tailed. Analysis of the prereversal phase of training for the 10 common sessions revealed a groups factor that approached significance,  $F(1, 18) = 3.07$ ,  $p = .09$ , and a significant Groups  $\times$  Sessions interaction,  $F(9, 162) = 4.96$ ,  $p < .01$ . There was no effect of sessions ( $p > .10$ ). Latencies were lower in 9 of the 10 sessions for win–shift (Mann–Whitney,  $Z = -3.55$ ,  $p < .01$ ) in this phase. Analysis of postreversal latencies for the first 10 common sessions revealed no overall group differences ( $p > .10$ ), no effect

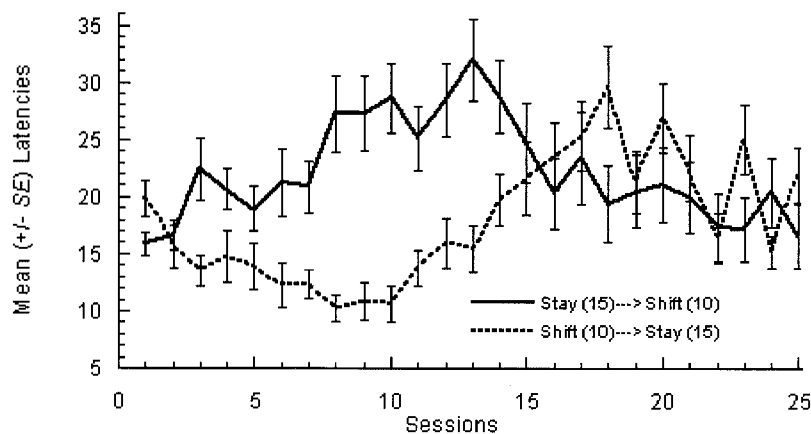


Figure 2. Mean ( $\pm$  SE) latencies for each session. Numbers in parentheses in legend indicate the number of sessions of training for each procedure.

of sessions ( $p > .10$ ), and a significant Groups  $\times$  Sessions interaction,  $F(9, 162) = 4.57$ ,  $p < .01$ . That interaction was composed of significant declines in latencies for the stay–shift group during win–shift training (Sessions 16–25; see Figure 2) and of significant increases in latencies for the shift–stay group during win–stay training (Sessions 10–25; see Figure 2;  $p < .05$ , for comparisons of the first three vs. last three sessions of training for both groups).

The analysis of order effects for latencies indicated no main effect for either procedure ( $p > .10$ ). There was a significant Sessions  $\times$  Groups interaction for win–stay,  $F(14, 252) = 2.05$ ,  $p < .05$ , but not for win–shift ( $p > .10$ ). The interaction for win–stay training was composed of significant latency increases during training for the stay–shift group ( $p < .01$ ) but not for the shift–stay group ( $p > .10$ ). The additional five training sessions under win–stay did not affect latencies for the stay–shift group ( $p > .10$ ) but did result in significantly lower latencies for the shift–stay group,  $t(9) = -3.13$ ,  $p > .01$ .

Perseverations were computed by determining the proportion of correct responses to each alternative (i.e., proportion of correct responses when left was correct and when right was correct) over the last five sessions for a given mouse. The absolute difference between these two proportions was then divided by the mean proportion of errorless trials for that mouse over that period. By this measure, higher proportions indicate greater perseveration. In the extreme case in which all of a mouse's correct responses were made to one alternative, the resulting ratio would be 1.0. Mice recorded more than three times as many perseverations during win–stay (averaged across both groups,  $M = .64$ ,  $SD = .33$ ) than during win–shift ( $M = .21$ ,  $SD = .17$ ),  $t(19) = 6.09$ ,  $p < .01$ .

Spontaneous alternations were measured as the mean proportion of alternations, defined as choice of the arm not chosen on the first run of a trial, across 25 trials (5 trials/session, 5 sessions). Averaged across five sessions, measures of spontaneous alternation did not correlate with errorless trials or latencies in either win–shift or win–stay,  $r(18) = -.23$  to  $.07$ ,  $p > .10$ , for all correlations. There were also no significant correlations observed when controls for extended spontaneous alternation training were instituted by using only first session alternations or the alternations obtained from the early portions of each session.

## Discussion

These results do not support the conclusion that mice prefer a win–stay strategy under conditions of aversive motivation. In this experiment, mice clearly learned a win–shift task more rapidly than a win–stay task under conditions of water escape. Moreover, there was no evidence of acquisition above chance levels during win–stay training for either group. In contrast, Means (1988) found that correct responses were higher for rats in a win–stay as compared with a win–shift water escape task. Additionally, whereas we found perseverations to be higher in win–stay than in win–shift, Means found higher levels of perseverations in win–shift as compared with win–stay.

It might be argued that the discrepancies between these results and those of Means (1988), Comer and Means (1989), and Mitchell et al. (1984) are principally due to species differences: Under aversive motivation, mice apparently prefer win–shift to win–stay strategies, whereas rats prefer win–stay strategies. The problem

with this interpretation, as noted earlier, is that there are exceptions to these sorts of generalizations. Additionally, there are numerous methodological differences between this and other studies, particularly the study by Means that used rats in a water escape procedure. Means's principal experiment (Experiment 1) studied rats in a between-subjects design that had a total of 20 acquisition trials (2 trials/session for 10 sessions). In the present study, mice received 100 trials at a minimum (10 trials/session) in a mixed reversal design. Means also used an extremely long 10-min ITI between sample and free-choice trials during which mice were removed from the apparatus. We used a 20-s ITI in which mice were run for all 10 trials within a session before the next mouse was run. There are other differences as well, including the apparatus used and procedural parameters used, such as the 60-s forced swim following incorrect choices in Means's study (Experiment 2).

These procedural differences suggest caution in interpreting differences between these studies to be a function of species differences. Naturally, the strength of the alternative, a procedure-dependent interpretation, depends on the ability of variations in procedural features to alter experimental outcomes. There are, indeed, a number of such examples related to win–shift and win–stay training, including a study by Goodlett, Nonneman, Valentino, and West (1988) that concerned the ability of rats to learn win–shift strategies under a variety of motivational and procedural parameters. These authors found that although rats rapidly acquired spatial T-maze alternation under conditions of food and water deprivation, they failed to acquire that same task under water escape motivation despite a number of procedural manipulations. Yet, when a different type of win–shift task was instituted, one similar to our win–shift procedure, rats rapidly demonstrated reliable acquisition under water escape motivation. When a win–stay water escape task was used that was similar to our win–stay task, however, rats demonstrated no reliable acquisition even after extended training. On this same point concerning the power of procedural variations, contrary to the usual findings, there are demonstrations of more rapid win–stay learning in rats using food reinforcement (Nakagawa, 1993; Reed, Skiera, Adams, & Heyes, 1996, Experiment 4).

It should be added that the exceptions to arguments based on species differences in win–shift/win–stay preferences parallel more general arguments concerning species differences in learning and intelligence. The fate of these arguments has often been that when careful manipulation of experimental parameters has taken place, what appeared as a qualitative difference between species is better seen subsequently as a function of the particular experimental parameters used in different investigations (e.g., Macphail, 1982).

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